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ABSTRACT

The significance of aquatic food resources for hominins is poorly understood, despite evidence of consumption as early as 1.95 million years ago (Ma). Here we present the first evidence of a non-human ape habitually catching and consuming aquatic crabs. Chimpanzees (*Pan troglodytes verus*) in the rainforest of the Nimba Mountains (Guinea) consumed freshwater crabs year-round, irrespective of rainfall or ripe fruit availability. Parties of females and offspring fished for crabs more than predicted and for longer durations than adult males. Across months, crab-fishing was negatively correlated with ant-dipping, suggesting a similar nutritional role. These findings contribute to our understanding of aquatic faunivory among hominins. First, aquatic faunivory can occur in closed forests in addition to open wetlands. Second, aquatic fauna could have been a staple part of some hominin diets, rather than merely a fallback food. Third, the habitual consumption of aquatic fauna could have been especially important for females and their immature offspring. In addition to providing small amounts of essential fatty acids, crabs might also be eaten for their micronutrients such as sodium and calcium, especially by females and young individuals who may have limited access to meat.

***Keywords*:** chimpanzee; aquatic faunivory; hominin evolution; freshwater crabs; Crustacea; Arthropoda

1. Introduction

Recent research suggests that aquatic resources were sometimes an important component of hominin diets (Braun et al., 2010; Archer et al., 2014). The earliest evidence of aquatic faunivory by hominins dates to the early Pleistocene (1.95 Ma) at

Koobi Fora, northern Kenya, and includes the consumption of turtles, crocodiles and fish (Stewart, 1994; Braun et al., 2010). It has been argued that regular consumption of aquatic fauna may have facilitated the initial onset of hominin brain growth in early *Homo* approximately 2 Ma (Joordens et al., 2014). Aquatic fauna would have provided essential long-chain polyunsaturated fatty acids (PUFAs), including docosahexaenoic acid (DHA) and eicosapentaenoic acid (EPA), which are required for optimal brain growth and function (Stewart, 2010; Joordens et al., 2014; but see Carlson and Kingston 2007). Furthermore, it has been proposed that hominins living in wetland habitats relied on aquatic resources as a seasonal fallback food at times of terrestrial food scarcity (Stewart, 1994, 2010; Archer et al., 2014).

Despite the potentially important impact that aquatic resource consumption might have had for hominins, little is known about the environmental conditions and demographic factors that could have influenced consumption of aquatic fauna. Here we report the first evidence of aquatic faunivory by chimpanzees (*Pan troglodytes*). The last common ancestor of *Pan* and *Homo* dates to approximately 6 – 8 Ma (Langergraber et al., 2012; Steiper and Seiffert, 2012; Amster and Sella, 2016), and was probably chimpanzee-like (Pilbeam and Lieberman, 2017; cf. Lovejoy et al., 2009). Thus, extant *Pan* are a possible proxy to gain new insights into the aquatic foraging strategies of hominins (Stewart, 2010). Our findings likely have more bearing on earlier hominins (e.g. *Ardipithecus* spp.) than on later taxa (e.g. *Homo* spp.), considering the greater similarities in brain size and habitat type between chimpanzees and earlier hominins (e.g. Robson and Wood, 2008; White et al., 2009).

Evidence for the consumption of aquatic fauna by non-human primates is sparse. In the wild, 20 primate species consume (some) aquatic fauna (Kempf, 2009; Russon et al., 2014). Most cases of aquatic faunivory are site-specific and likely

76 influenced by human activities (Russon et al., 2014), with the notable exception of tool-
77 assisted foraging on aquatic fauna by long-tailed macaques (*Macaca fascicularis*
78 *aurea*) in Thailand (Gumert and Malaivijitnond, 2012). Among the great apes in
79 particular, evidence for the consumption of aquatic fauna is rare and no previous
80 evidence exists for chimpanzees (Russon et al., 2014). By contrast, chimpanzees are
81 well known for consuming aquatic flora, such as the algae obtained from ponds
82 (Nishida, 1980; Sakamaki, 1998), sometimes with the use of tools (Matsuzawa et al.,
83 1996; Devos et al., 2002; Boesch et al., 2017).

84 We found that chimpanzees (*P. t. verus*) at the Seringbara study site in the
85 Nimba Mountains of Guinea, West Africa, regularly consumed freshwater decapod
86 crustaceans, which we term 'crab-fishing'. The chimpanzees searched for crabs in
87 shallow, permanent, watercourses in this mountainous rainforest site by using their
88 fingers to scrape and disturb the stream-bed (Fig. 2; Supplemental Online Material
89 (SOM) Videos 1, 2, 3).

90 To address dietary function, we report the nutritional value of freshwater crabs,
91 and assess the relationship between crab-fishing and the availability of ripe fruits and
92 ants, which are two important components of the chimpanzee diet at this site. Ripe fruit
93 is the food most frequently eaten by chimpanzees, although their diet is best described
94 as omnivorous (Wrangham et al., 1998). At Seringbara, the insects most commonly
95 eaten by chimpanzees are army ants (*Dorylus* spp.), whereas termite consumption is
96 absent (Koops et al., 2013; Koops et al., 2015). We compare the energy content and
97 nutrient concentrations of crabs with those of army ants in order to assess the relative
98 dietary importance of crabs and insect prey at Nimba. In addition, we investigate
99 variation among sex and age classes in the frequency and duration of crab-fishing, as
100 well as in the catch rates of crabs.

To suggest insights into what may have driven the consumption of aquatic fauna among hominins, our study thus addresses questions regarding the environmental context, demography, and dietary function of aquatic faunivory by chimpanzees.

2. Methods

2.1 Study site

The Seringbara study site (N 07.37˚; W 08.28˚) is located in the Nimba Mountains in the southeastern part of the Republic of Guinea, West Africa. The site covers about 25 km^2 of steep hills and valleys located 6 km from Bossou, where a small community of chimpanzees has been studied for over 30 years (Matsuzawa et al., 2011). The Seringbara chimpanzees range between approximately 600 - 1400 m altitude (Koops, unpublished data). The Nimba region has been surveyed intermittently since 1992 (Matsuzawa and Yamakoshi, 1996; Shimada, 2000; Humle and Matsuzawa, 2001). The Nimba Mountains show great topographical diversity, ranging from rocky peaks and high altitude meadows to deep valleys and rounded hilltops. The steep hills are covered by dense primary tropical forest interspersed with forested valleys. Numerous constant, fast-flowing watercourses cut through the forest, making the Nimba Mountains an important water catchment area (World Conservation Monitoring Centre, 1992). The climate is characterized by a rainy season starting in February/March and ending in November/December and a 3-month dry season (i.e. monthly rainfall <70 mm). Since 2003, researchers and field assistants have maintained a near-constant presence at the study site, except for a break during an Ebola epidemic (2014 – 2018). The Seringbara chimpanzees remain largely unhabituated to human observers. The extremely mountainous terrain makes habituation of these chimpanzees very difficult. The study site has at least two chimpanzee communities, based on repeated direct observations

126 and motion-triggered camera images of known individuals (Koops, personal
127 observation) and genetic evidence (Koops et al., 2012). For more information on the
128 Seringbara study site, see Koops (2011).
129
130 *2.2 Study period*
131 We collected crab-fishing data from February 2012 until April 2014. KK collected data
132 with the help of local field assistants and an international team of research assistants.
133
134 *2.3 Monitoring of crab sites and control sites*
135 We set up motion-triggered cameras (Bushnell Trophy Cam XLT 8MP Trail Camera)
136 at all four crab-fishing sites discovered between February 2012 and May 2013 (Table
137 1, Fig. 1). All four crab-fishing sites were monitored continuously from the various
138 times of their discovery until April 2014. The sites were characterized by freshly dug
139 pools with traces of chimpanzee digging activity, such as finger marks and piles of dug
140 out sand and stones. We placed two (opposite) cameras at each crab-fishing site to
141 obtain maximum coverage. In addition, we monitored eight 'control sites' throughout
142 the home range of the chimpanzees using one camera at each site (Fig. 1). Control sites
143 were placed on randomly-selected chimpanzee trails with signs of active use (e.g.
144 knuckle prints) and without any feeding trees, or other food sources, recorded nearby.
145 Data on chimpanzee parties from control sites were used to compare party size and
146 party type (i.e. female(s) only, female(s) and offspring, male(s) only, mixed sex) with
147 crab-fishing sites. Control site data were collected between April 2011 – March 2014
148 (N = 1577 monitoring days, mean = 197 days per site) with 1 – 4 control site(s)
149 monitored in each month (see SOM Table S1). Recent research has shown that targeted
150 placement of cameras (e.g. on chimpanzee trails) increases detection probability and is

151 recommended in order to obtain data on party size and composition (Després-
152 Einspenner et al., 2017).

153 Motion-triggered cameras provided information on the number of chimpanzee
154 parties visiting, as well as the number of chimpanzee parties fishing for crabs (Table
155 1). In addition, we collected data on party size (excluding infants), party type, and the
156 sex/age class of individuals visiting and fishing for crabs. Chimpanzees visiting the
157 same site within 1 hour of each other were considered as part of the same party. The
158 crab-fishing duration of a party was based on the start time of the first individual to
159 begin crab-fishing and the end time of the last individual to finish crab-fishing. We
160 determined catch rates for chimpanzees belonging to the different sex and age classes
161 based on the number of hand-to-mouth movements followed by chewing (Fig. 2) per
162 minute. Only videos with at least one minute of a continuous unobstructed view of both
163 hands and mouth of a focal chimpanzee were included as a 'fishing session' in our
164 analyses of catch rates.

165

166 *2.4 Fruit availability*

167 To monitor the temporal variation in ripe fruit availability, we set up two 500 m
168 transects (N – S and E – W) on each of 4 – 6 hills and valleys (depending on the study
169 period). From January – December 2012 the total transect length was 4 km. From
170 January 2013 – March 2014 the total transect length was 6 km, as we added 2 km of
171 additional transect length in January 2013. We located transects according to a stratified
172 random design across the study site. We tagged and measured the DBH (diameter at
173 breast height) of all trees and vines belonging to confirmed chimpanzee food species
174 with a DBH $\geq$ 10 cm and with the trunk midpoint within 5 m to each side of the transect
175 line. Chimpanzee food tree species were identified based on seeds and fruit remains

recorded in fecal samples (N = 1281) and on direct observations of chimpanzees feeding since 2003. Between January 2012 and April 2014, we noted the presence of ripe fruit during the first half of each month in each tagged tree or vine. Fruit was scored as: 0) Fruit absent; 1) 1-25% of canopy containing fruit; 2) 26-50%; 3) 51-75%; 4) 76-100%. We calculated a monthly fruit availability index (FAI) for chimpanzee food species (2012: N = 45, 2013 - 2014: N = 53). The FAI provides an estimate of habitat-wide ripe fruit abundance for chimpanzees (following Chapman et al., 1994) and is calculated with the following formula (sensu Hockings et al., 2010; Koops et al., 2013; Koops et al., 2015; Takemoto, 2004):$FAI = [\Sigma (P_i \times F_i) / \Sigma (P_i \times 4)] \times 100$

where FAI is the fruit availability index (%), i.e. percentage of chimpanzee food trees (along the transects) providing food in a given month. P_i is the basal area (cm^2) of each individual chimpanzee food tree 'i' (N = 576 trees in 2012, N = 800 trees in 2013 – 2014), calculated as $P_i = [0.7854 \times DBH^2]$. F_i is the fruiting score (scores: 0 – 4, as explained above) of each chimpanzee food tree. As such, the numerator of the FAI formula outlines the sum of chimpanzee food trees providing fruit in a given month, as measured by the basal area and fruiting score for each tree. The denominator specifies the maximum number of chimpanzee food trees that could be providing fruit in a given month, as measured by the basal area and maximum fruiting score (i.e. 4) for each tree.

2.5 Rainfall

Rainfall was recorded daily at 17.30h with a manual rain gauge at our base camp (Madei Camp), which is located at an altitude of 670 m.

2.6. Ant-dipping

200 To obtain information on the tool-assisted consumption of army ants (i.e. ant-dipping)
201 by the chimpanzees, we collected fresh (<2 days old) fecal samples below recently
202 occupied nests and along trails while tracking chimpanzees. We recorded a total of 889
203 fecal samples between March 2012 – April 2014 with on average 37 samples collected
204 per month (range: 8 – 145 samples, median = 24, SEM = 6.9). We pre-soaked fecal
205 samples in water, sieved them with a 1-mm mesh (sensu McGrew et al., 2009) and
206 scored army ant remains as present or absent.
207
208 *2.7 Crab availability plots*
209 We measured the availability of crabs by randomly placing 5 plots (1 m x 1 m) at each
210 of the four crab sites (total plots: N = 20) in November 2013. We measured crab
211 availability at the transition between wet and dry season in order to obtain a
212 representative measure for the whole year. We established a protocol in which four
213 people spent 5 minutes simultaneously at each plot searching and counting all crabs.
214 We assigned the recorded crabs to three size classes (using a ruler): Small: <2 cm
215 carapace length (CL), Medium: 2 – 5 cm CL, and Large: >5 cm CL.
216
217 *2.8. Nutritional analyses*
218 A subset of crabs (N = 27 total, 42% of crabs recorded) from availability plots at the
219 four sites (i.e. all crabs recorded at Sites 1, 3 and 4; N = 11, or 23% of crabs recorded
220 at Site 2) were stored in 95%-ethanol at room temperature and kept for later nutritional
221 analyses in the lab. We analyzed the samples at the Primate Nutritional Ecology Lab at
222 Hunter College in New York, USA. First, ethanol was evaporated off of the samples,
223 and the samples were dried in a desiccator at room temperature for 12 hours. They were
224 then ground with a mortar and pestle. The crabs were then analyzed for their fat, chitin,

protein, energy and mineral concentrations similarly to the ants analyzed by Isbell et al. (2013). Crude fat was analyzed via ether extract using an ANKOM XT15 fat analyzer. Chitin, which comprises a major portion of the exoskeleton of invertebrates was estimated using acid detergent fiber (Finke, 2002; Bryer et al., 2015). Nitrogen concentrations (N) were analyzed via combustion with a nitrogen (N) analyzer (Leco TruSpect N). This total N was multiplied by 6.25 to estimate crude protein. Gross energy was estimated by using an IKA bomb calorimeter. Mineral concentrations were estimated by using an iCAP 700 Series ICP Spectrometer after ashing at 500 ºC in a muffle furnace as in Rothman et al. (2006). Dry matter was calculated by drying a subsample of each sample of crabs in a 105 ºC oven for 4 hours and estimating the atmospheric moisture lost during this process (Goering and Van Soest, 1970; Rothman et al., 2012). Aside from gross energy which is reported as kcal per 100 g of dry mass, nutrient estimates are reported as percentage of dry matter. We analyzed crude protein, crude fat and acid detergent fiber (ADF) for the three size classes separately (Table 2). We did not have adequate amounts of sample for the small size class to analyze gross energy separately, and for the small and medium size class to analyze mineral concentrations separately, since each analysis uses about 0.5 – 1.0 g of sample weight.

2.9. Ethics Statement

This research was non-invasive, complied with the laws of Guinea, and was approved by the Direction General de la Recherche Scientifique et l'innovation Technologique (DGERSIT). Moreover, this research adhered to guidelines as set down by the Division of Biological Anthropology, University of Cambridge.

2.10. Data analyses

We tested the data for normality using normal probability plots and a Kolmogorov-Smirnov test (Field, 2013) and we used parametric and non-parametric tests accordingly. All analyses were performed two-tailed and significance levels were set at 0.05. We performed statistical tests in IBM SPSS version 21.0 To analyze the relationships between crab-fishing and rainfall, FAI, and ant-dipping (see below), we used chimpanzee visiting rate of crab-fishing sites (i.e. parties visiting per day per site, including parties without confirmed crab-fishing), rather than crab-fishing rates (i.e. parties visiting per day per site, only with confirmed crab-fishing), since monthly crab-fishing rates were not normally-distributed whereas monthly visiting rates were. Visiting rates and crab-fishing rates showed a strong positive correlation ($r_s = 0.91$, $P < 0.0001$). We used a T-test to compare monthly visiting rates between the first and second monitoring year. After checking the assumptions (incl. multivariate normality), we used a multiple linear regression to investigate which predictors affect visiting rates of crab-fishing sites: rainfall, FAI, and/or ant-dipping (i.e. proportion of fecal samples containing army ant remains per month).

We used Mann-Whitney U tests to compare the size of crab-fishing parties and sex ratios to control site parties. We used Chi-square tests to compare the proportions of the different party types at crab-fishing and control sites. Subsequently, we determined the party type categories in which the proportions of parties differed from expected proportions, based on marginal totals (i.e. totals for each row and column) of the different party types. We inspected the adjusted residuals (adj. res.), which are approximately normally distributed. As there were four comparisons run, to minimize the risk of Type I errors, we controlled for multiple testing by means of the improved Bonferroni procedure (Hochberg, 1988). We used a Chi-square test, followed by inspection of adjusted residuals with Bonferroni correction (i.e. 4 comparisons), to

compare time spent crab-fishing across party types. We used Kruskal-Wallis tests to compare visit duration across party types and to compare catch rates and participation in crab-fishing across age/sex classes. 'Participation' in crab-fishing was calculated as the percentage of individuals (of a particular age/sex class) present in a party and also fishing for crabs. For example, if a crab-fishing party contained four adult males, and two adult males fished for crabs, the adult male participation for this party would be 50%. We used Mann-Whitney U tests with Bonferroni correction to determine which age/sex classes differed in crab-fishing participation and catch rates, and to compare catch rates between seasons. We used Kruskal-Wallis tests to compare catch rates and visiting rates across the four sites, followed by Mann-Whitney U tests with Bonferroni correction. Site 4 had only one catch rate value and was excluded from this analysis.

3. Results

3.1. Discovery of crab-fishing

On the 25th of February 2012, we encountered the first indirect evidence of chimpanzees feeding on freshwater crabs. After following fresh chimpanzee traces (i.e. knuckle prints, feces, and feeding remains) for about 45 min, we encountered a small creek with 'pools' of standing water. Traces of recent digging activity (i.e. finger marks and piles of dug out materials) indicated that the pools were freshly excavated. After setting up two motion-triggered cameras at this site (Site 1) on the 18th of March 2012, we captured the first footage of crab-fishing by chimpanzees on the 23rd of March 2012. We subsequently discovered three additional crab-fishing sites in June 2012, January 2013, and June 2013 (Table 1), and we monitored all four sites until April 2014. The four crab-fishing sites were located between 720 – 875 m altitude.

299 On the 4th of August 2012, we discovered fresh feeding remains at one of our
300 monitored crab-fishing sites (Site 2, Fig. 3a). On the 18th of May 2013, we discovered
301 and collected another set of fresh crab-feeding remains (Site 1, Fig. 3b). They were
302 subsequently identified as belonging to two species of potamonautid freshwater crabs
303 (the common creek crab, *Liberonautes latidactylus* (De Man, 1903), and the lobster-
304 claw crab, *L. rubigimanus* (Cumberlidge and Sachs, 1989; Cumberlidge, 1999;
305 Cumberlidge and Huguet, 2003)).
306 We monitored chimpanzee parties for a total of 71 site-months (Table 1).
307 During this time 240 parties visited crab-fishing sites, and in 75.4% of these visits (N
308 = 181) at least one member of the party was filmed attempting to fish for crabs by
309 disturbing the shallow stream-bed with their fingers. This estimate of crab-fishing
310 frequency is a minimum, because in the remaining 24.6% of visits (N = 59), there was
311 either poor visibility (e.g. heavy rain, fogged-over camera lenses) or (some) individuals
312 moved out of view of the cameras into positions where any crab-fishing could not be
313 verified. Of the 181 crab-fishing parties, 177 parties had enough information on all the
314 individuals present in the party to be used for further analyses on party characteristics
315 (e.g. party size, party type).
316 Overall monthly visiting rates of the crab-fishing sites increased significantly
317 (i.e. doubled) in the second as compared to the first monitoring year (0.07 vs. 0.14
318 parties/day/site, T-test: -2.946, P = 0.007). There was a suggestion of visiting rates
319 differing across sites (Kruskal-Wallis test: $N_1 = 25$, $N_2 = 21$, $N_3 = 14$, $N_4 = 10$, H =
320 8.59, df = 3, P = 0.035), but Mann-Whitney U post-hoc comparisons failed to show
321 significant differences.
322
323 *3.2. Relationship of crab-fishing related to rainfall, fruit availability, and ant-dipping*

In a multiple linear regression using rainfall, FAI, and ant-dipping frequency, the only significant predictor of visiting rate at crab-fishing sites was ant-dipping ($R^2 = 0.193$, $F_{1,21} = 5.011$, standardized ß = -0.439, P = 0.036). Chimpanzees visited crab-fishing sites more often when they dipped less for ants (Fig. 4).

3.3. Which parties (size, type) fish for crabs?

The size of crab-fishing parties (mean = 3.2 individuals, N = 177) did not differ significantly from parties at control sites (mean = 3.7 individuals, N = 155) (Mann-Whitney U test: z = -0.381, P = 0.703). However, the proportions of different party types did vary between the 4 crab-fishing sites and 8 control sites (Chi-square test: $\chi^2 = 17.436$, df = 3, P < 0.001, Fig. 5). Specifically, crab-fishing parties contained mother-offspring pair(s) more often than at control sites (adj. res. = 2.8, P < 0.01), and were all-male less often than at control sites (adj. res. = 3.6, P < 0.001). In keeping with those findings, the sex ratio of crab-fishing parties was significantly lower than the sex ratio of control parties (i.e. crab-fishing parties had fewer males per female) (0.23 vs. 0.39; Mann-Whitney U test: z = -3.762, P < 0.0001).

3.4. Which parties spend most time crab-fishing?

The overall mean visit duration at crab-fishing sites was 20.2 min (range: 1 - 166, SEM = 2.3). The mean visit duration for different party types (female(s) only: 6.3 min, female(s) and offspring: 26.9 min, male(s) only: 16.2 min, mixed: 14.9 min) did not differ significantly (Kruskal-Wallis Test: $N_1 = 20$, $N_2 = 92$, $N_3 = 12$, $N_4 = 53$, H = 5.387, P = 0.146). However, when we compared time spent crab-fishing (% parties) by parties composed solely of female(s) and offspring to the time spent crab-fishing by other party types, we found a significant difference (Chi-square test: $\chi^2 = 12.524$, df = 3, P = 0.006,

Fig. 6). Female(s) and their offspring more often spent over an hour crab-fishing, compared to other party types (adj. res. = 3.5, P = 0.001).

3.5. Which chimpanzee age/sex classes fish for crabs?

The age/sex classes (i.e. adult males, adult females, adolescents, juveniles) differed significantly in their crab-fishing participation (i.e. % individuals crab-fishing) when in crab-fishing parties (Kruskal-Wallis test: $N_{\text{parties with adult male(s)}} = 57$, $N_{\text{parties with adult female(s)}} = 158$, $N_{\text{parties with adolescent(s)}} = 67$, $N_{\text{parties with juvenile(s)}} = 129$, $H = 28.201$, $df = 3$, $P < 0.0001$). First, adult males were less likely than adult females or juveniles to fish for crabs (mean: 57% adult male participation vs. 75% adult female participation, Mann-Whitney U test: $z = 3.359$, $P = 0.001$; mean: 57% adult male participation vs. 87% juvenile participation, $z = 5.411$, $P < 0.001$). Second, adult females were less likely to fish for crabs than juveniles (mean: 75% adult female participation vs. 87% juvenile participation, $z = 2.775$, $P = 0.006$). Adolescents (mean: 72% participation) did not differ significantly from other age/sex classes.

3.6. Do crab catch rates differ across chimpanzee age/sex classes, seasons and sites?

We determined catch rates for 145 fishing sessions in 94 crab-fish parties. The mean catch rate was 1.71 catches per minute of crab-fishing (range: 0 – 9, Median = 1.5). Adult males (mean = 1.60), adult females (mean = 1.56), adolescents (mean = 2.18) and juveniles (mean = 1.83) did not differ significantly in their catch rates (Kruskal-Wallis test: $N_{\text{adult females}} = 58$, $N_{\text{adult males}} = 37$, $N_{\text{adolescents}} = 19$, $N_{\text{juveniles}} = 31$, $H = 4.616$, $df = 3$, $P = 0.202$). There was no difference in catch rates between the dry and the wet season (Mann-Whitney U test: $N_{\text{dry}} = 62$, $N_{\text{wet}} = 83$, $z = -0.315$, $P = 0.753$). There was a difference in catch rates across Sites 1, 2 and 3 (Kruskal-Wallis test: $N_{\text{Site1}} = 60$, N_{Site2}

374 = 44, N_{Site3} = 40, H = 8.214, df = 2, P = 0.016), with catch rates being higher at Site 2
375 compared to Site 1 (Mann-Whitney U test: z = 2.421, P = 0.015).
376
377 *3.7. Crab availability*
378 The mean crab availability was 3.2 crabs/m^2 (Site 1 = 1.8, Site 2 = 9.6, Site 3 = 0.4, Site
379 4 = 1.0). The majority of crabs belonged to the small size class (N = 48, 75%), followed
380 by the medium size class (N = 12, 19%) and the large size class (N = 4, 6%).
381
382 *3.8. Nutritional value of crabs*
383 We analyzed the energy content and nutrient concentrations for crabs (Table 2), and
384 compared these values to published nutrient concentrations of army ants eaten by
385 chimpanzees in Cameroon (Deblauwe and Janssens, 2008). Gross energy of large crabs
386 was similar to army ants. However, the analysis of army ant gross energy was reported
387 on fresh matter basis (Deblauwe and Janssens, 2008), which includes moisture, and
388 thus is not directly comparable to crab gross energy that is presented on a dry matter
389 basis. Crabs stood out in terms of high concentrations of calcium and low
390 concentrations of iron and zinc as compared to army ants.
391
392 **4. Discussion**
393 This study describes a newly discovered chimpanzee behavior termed crab-fishing,
394 which constitutes the first evidence of chimpanzee aquatic faunivory. Chimpanzees in
395 the Nimba Mountains fished for crabs year-round, irrespective of rainfall or availability
396 of ripe fruit. Crab-fishing was negatively correlated with ant-dipping. Moreover, sex
397 and age classes differed in their reliance on this aquatic resource. Females and
398 dependent offspring fished for crabs more than expected, whereas parties with only

399 males did so less than expected, based on comparisons between four crab-fishing and
400 eight control sites. Females and dependent offspring also fished for the longest
401 durations. Among individuals in a crab-fishing party, immature individuals were the
402 most likely to fish for crabs, whereas adult males were the least likely to do so. We use
403 these findings to address three gaps in our current knowledge regarding aquatic
404 faunivory in our hominin ancestors, i.e. environmental context, demography, and
405 dietary function.
406
407 *4.1. Crab-fishing a recent innovation?*
408 We discovered crab-fishing in 2012, despite the chimpanzees at the Seringbara study
409 site being intensively studied since 2003. Chimpanzee rates of visiting crab-fishing sites
410 doubled in the second monitoring year compared to the first. Why crab-fishing was not
411 observed until 2012 is unclear. It could have occurred undetected, or it might have been
412 absent.
413 It would be surprising if, for nine years prior to 2012, crab-fishing had occurred
414 without researchers detecting it. Search efforts for chimpanzee traces at the study site
415 were extremely thorough, with two to four teams in the forest on most days. The
416 research team was expert at finding chimpanzee traces, so it is unlikely that they would
417 have missed the obvious disturbance left behind after chimpanzees crab-fish.
418 Furthermore, the crab-fishing sites were located in a heavily surveyed area, close to our
419 base camp.
420 Therefore, it is possible that crab-fishing may be a recent innovation in the
421 chimpanzees of the Nimba Mountains, begun only shortly before we discovered it. If
422 so, it could have been introduced by an immigrant female, or it could have been
423 invented. An introduction by an immigrant female could help explain the limited

participation in crab-fishing by adult males in Nimba (see below), which mirrors observations in the Kasekela community in Gombe (Tanzania) where adult males did not engage in ant-fishing after the introduction of the behavior by an immigrant female (O'Malley et al., 2012). Future research may shed light on this problem by showing whether crab-fishing spreads further in Nimba, much as moss-sponging has been shown to spread among Budongo chimpanzees (Hobaiter et al., 2014).

4.2. Environmental context

Evidence for the consumption of aquatic fauna by hominins has come mostly from lakeshore or marine habitats (e.g. Braun et al., 2010; Archer et al., 2014). This pattern of archaeological finds could be linked to fossils being preserved and recovered better in wetlands than forests. The four crab-fishing sites that we studied in the Nimba Mountains were all in primary riverine forest, characterized by shallow permanent streams with sandy, rocky soil, and some larger boulders (see SOM Videos 1, 2, 3). Our data thus show that aquatic fauna can be regularly exploited in a rainforest habitat with only small streams.

Seasonality has been proposed to have played an important role in the use of aquatic resources by hominins (Stewart, 2010), with intensified use of wetlands and consumption of aquatic fauna by hominins being predicted during dry periods when dry-habitat foods are scarce (Stewart, 2010; Archer et al., 2014). During our study, chimpanzees fished for crabs during all 25 observation months. Surprisingly, there was no relationship between crab-fishing and monthly rainfall. Nor was there a difference in crab catch rates between the dry and the wet season: even in the dry season, the streams held enough water to provide suitable living conditions for freshwater crabs. In sum, aquatic fauna was not a seasonal food source for chimpanzees, but a year-round

449 part of their diet.

450

451 *4.3. Demography*

452 The chimpanzees' reliance on crab-fishing varied among age-sex classes. Parties
453 consisting of adult female chimpanzees and their dependent offspring fished for crabs
454 more often than other party types, and male-only parties were the least likely to fish for
455 crabs. Females and youngsters also fished for crabs for the longest durations, regularly
456 exceeding an hour of foraging time. Moreover, juvenile visitors were the most likely to
457 fish for crabs, whereas adult male visitors were the least likely to do so. Hence, it seems
458 that the dietary importance of this aquatic resource differs according to an individual's
459 sex and age. We note that a shortcoming of camera-trap studies is that some individuals
460 are likely to be missed and camera trap party size should thus be considered a minimum
461 estimate of true party size (McCarthy et al., 2018). Moreover, our study had only eight
462 control sites, yielding 155 parties used for assessing average party composition. A more
463 reliable assessment of age and sex class differences in crab-fishing will be possible with
464 direct observations of habituated study subjects.

465 In addition to possibly providing unusual nutritional benefits (see below), crab-
466 fishing may be particularly well suited to females with dependent offspring because it
467 is less risky than some other methods of eating animals. Although large crabs can inflict
468 painful pinches with their powerful claws (Koops, personal observation), the majority
469 of crabs (75%) found in Nimba posed little danger to chimpanzees because they were
470 small (<1cm CL). Hence, mothers with infants could let their youngsters practice
471 fishing for abundant small crabs without risk. In this respect, crab-fishing contrasts with
472 the high-risk activity of foraging on aggressive army ants, a highly gregarious and
473 mobile prey that can inflict numerous painful bites on chimpanzees (Humle et al.,

474 2009). Thus, the benefits of freshwater crabs as a food source for females with
475 immature offspring may include both nutritional and behavioral components.
476
477 *4.4. Nutrition*
478 Previous reports of non-human primate crab consumption included tarsiers (*Tarsius*
479 *bancanus, T. syrichta*), capuchin monkeys (*Cebus apella, C. libidinosis*), squirrel
480 monkeys (*Saimiri sciureus*), vervet monkeys (*Cercopithecus aethiops*), macaques
481 (*Macaca fascicularis, M. fuscata, M. siberu*) and baboons (*Papio anubis, P.*
482 *cynocephalus, P. ursinus*), as reviewed in Russon et al. (2014).
483 Nimba chimpanzees fished for crabs irrespective of how much ripe fruit was
484 present. A multi-year follow-up study of crab-fishing is needed to confirm whether this
485 finding holds across subsequent years. Long-tailed macaques (*M. fascicularis*), have
486 been found to rely more on aquatic fauna when ripe fruit is less abundant (Yeager,
487 1996; Malaivijitnond et al., 2007). Our findings suggest that, for chimpanzees in the
488 Nimba Mountains, crabs may be an important year-round food source, possibly acting
489 as a protein, lipid or mineral supplement to their fruit-based diet. We acknowledge that
490 availability of crabs may vary across the year (e.g. dry vs. wet season), and that
491 nutritional content may also vary across the year and between crabs of different size
492 classes. To address these potential variations, additional year-round data collection is
493 required.
494 Our results showed that chimpanzees fished more for crabs when they foraged
495 less for army ants. Army ant consumption at Nimba is largely opportunistic (Koops et
496 al., 2015), whereas crabs appear to be permanently available, so crab-eating plausibly
497 increases in response to low ant availability. Nutritional analyses revealed that gross
498 energy and sodium values in (large) crabs were similar to those in army ants. In

addition, calcium concentrations for (large) crabs were higher than for army ants, whereas iron and zinc concentrations were lower. We did not analyze mineral concentrations of small crabs as our sample mass was too small. However, it is reasonable to assume that the ratio of carapace to body is similar for large and small crabs, because the percentage of ADF was similar across size classes (Table 2) and ADF is considered an approximate measure of the chitin in carapace.

Why do Nimba chimpanzees eat crabs? One hypothesis is that crabs may be a reliable year-round available source of sodium, which can be a limiting resource for primates living in the tropics (e.g. Rode et al., 2003; Rothman et al., 2006). At many study sites apes seek out and consume unusual sodium sources such as decaying wood (Rothman et al. 2006; Venable et al., in prep.), rotting piths (Reynolds et al. 2009), exotically introduced *Eucalyptus* bark (Rothman and Bryer, 2019), and swamp foods (Magliocca and Gautier Hion, 2002) to meet sodium needs. It is possible that these crabs act as mineral supplements similar to these plant-based foods, or the insects that many primates consume (Rothman et al., 2014). Moreover, female chimpanzees may need more salt than males, since females generally have less access to meat (Fahy et al., 2013; Gilby et al., 2017). The need for salt could also explain the previously reported female-bias in insectivory (McGrew, 1979; Hiraiwa-Hasegawa, 1989). Moreover, at Kanyawara (Uganda), chimpanzees ingest wood to obtain salt, a behavior which is also female-biased (Venable et al., in prep.). Similarly, crab-fishing is biased towards females and their offspring, which may in turn be due to a potentially reduced access to salt through meat-eating for female chimpanzees and immatures.

A second hypothesis is that crabs are a source of calcium. Calcium is essential for both pregnant females and fast-growing immatures (human studies: Johnston et al., 1992; Mosha et al., 2016). The calcium concentrations of crabs are particularly high

per unit weight (Table 2), therefore possibly serving as a source of calcium for pregnant and nursing females and their dependent offspring. Calcium concentrations are higher in the carapace of crabs compared to their internal organs (Bilgin and Fidanbaş, 2011), which would make eating entire crabs nutritionally beneficial in terms of calcium. The actual digestibility of chitin for chimpanzees is as yet unknown (O'Malley and Power, 2012), but while research has shown that the human gastrointestinal tract contains chitinase (Paoletti et al., 2007), this does not mean that chimpanzees can digest chitin (Janiak, 2016). It is noteworthy, however, that there were no crab carapace remains found in chimpanzee feces in this study.

A third hypothesis is that crabs may be an important source of PUFAs such as DHA. The DHA concentrations of freshwater crab species obtained from the literature are high (Wan Rosli et al., 2012; Das et al., 2015; Islam et al., 2017), and may be indicative of high DHA concentrations in African freshwater crabs. DHA is considered an essential nutritional compound for pregnant and nursing mothers and young children because it is required for proper brain development and function (Birch et al., 2000; Das et al., 2015). Against this, the total amounts of PUFA ingested by chimpanzees from crab-fishing are unknown, and are probably small. Furthermore, some authors challenge the importance of dietary DHA, since conversion of alpha-linolenic acid, available in a variety of terrestrial resources, into DHA could potentially be sufficient for normal brain development (Carlson and Kingston, 2007). Hence, while freshwater crabs may provide an important source of DHA for pregnant or nursing female chimpanzees and immature offspring, future research on the nutrients in African freshwater crabs in comparison to other components of the chimpanzees' diet is needed to distinguish between these three hypotheses.

549 *4.5. Significance of crabs for chimpanzees*

550 Whether or not crab-fishing by chimpanzees is a recent innovation at Seringbara, it
551 appears to be a rare behavior given that it has not yet been observed at other chimpanzee
552 study sites. Freshwater crabs are widespread and abundant in West African forests
553 (Cumberlidge, 1999), which makes the absence of crab-fishing at other chimpanzee
554 study sites puzzling. One possibility is that crabs are not easily obtained at other sites,
555 because streams are perhaps more shallow at Nimba. However, evidence of crab
556 consumption by baboons at Gashaka (Nigeria), in a forest where chimpanzees also
557 occur, suggests otherwise (Sommer et al., 2016). Another possibility is that meat-eating
558 is limited at Seringbara (i.e. observations of chimpanzees hunting squirrels only), since
559 all monkey species present in the Nimba Mountains are under severe pressure from
560 hunting by humans (Koops, personal observation), potentially leading to a more
561 important role of invertebrates in the diet. Army ants are indeed an important year-
562 round part of the Nimba chimpanzee diet, with particularly high proportions of fecal
563 samples containing army ant remains (36%) compared to other sites (Koops et al.,
564 2013). Crab-fishing might thus provide nutrients that in other populations are provided
565 more often by vertebrate prey.

566

567 *4.6. Pathogen risk associated with crab consumption*

568 The two large species of freshwater crabs that are consumed by chimpanzees in the
569 Nimba region (*Liberonautes latidactylus* and *L. rubigimanus*) are also commonly eaten
570 by humans (Cumberlidge and Huguet, 2003). The former species is a known second
571 intermediate host of *Paragonimus uterobilateralis* in this part of West Africa (Sachs
572 and Cumberlidge, 1990). The crabs carry an infective stage (metacercaria) of the
573 parasite (Voelker, 1973; Sachs and Voelker, 1982; Monson et al., 1983; Sachs et al.,

574 1986). As a result, human lung fluke disease (paragonimiasis) is endemic to many areas,
575 including Guinea, Liberia, and Ivory Coast (Sachs and Cumberlidge, 1988).
576 A number of African non-human primates, i.e. drills (*Mandrillus leucophaeus*),
577 red-capped mangabeys (*Cercocebus torquatus*), and pottos (*Perodicticus potto*), also
578 eat freshwater crabs. Some of these primate species have confirmed lung fluke
579 infections (Voelker and Vogel, 1965; Sachs and Voelker, 1975; Voelker and Sachs,
580 1977; Friant et al., 2015). The crabs, being second intermediate hosts of *Paragonimus*,
581 harbor the only larval stage of the parasite capable of infecting the definitive host
582 (Voelker et al., 1975). The Nimba chimpanzees that consume freshwater crabs are thus
583 also at risk of contracting lung fluke disease. The presence of the parasite can be
584 assessed by examining fecal samples for *Paragonimus* eggs, which are identifiable by
585 morphology and molecular analyses (Friant et al., 2015).
586
587 *4.7. Implications for hominin aquatic faunivory*
588 Our findings suggest three points for the interpretation of the consumption of aquatic
589 fauna by hominins. First, the fact that forest-living chimpanzees, can fish for crabs
590 means that systematic reliance on aquatic faunivory is not restricted to lakeshore, river
591 margin, and coastal ecotones, as has been generally assumed (e.g. Erlandson, 2010;
592 Shabel, 2010). Possibly aquatic fauna were exploited by hominins living in a closed,
593 forested environment, such as *Ardipithecus* spp. and some populations of early
594 *Australopithecus* spp. (White et al., 2009; cf. Cerling et al., 2015).
595 Second, crab-fishing by chimpanzees in Nimba was not linked to fruit
596 availability. This indicates that the importance of aquatic faunivory for hominins would
597 not necessarily have varied seasonally.

598 Third, crab-fishing was disproportionately performed by adult females and their
599 dependent offspring, whereas adult males participated the least. Possibly aquatic
600 faunivory in hominins may have been similarly biased towards females and immatures.
601 This hypothesis can be explored by understanding the factors promoting increased crab-
602 fishing by females and young.
603
604 **5. Conclusions**
605 We found that apes living in a rainforest can exploit aquatic fauna, which implies that
606 forest-living hominins could have done likewise in similarly forested environments.
607 Our evidence suggested that mothers and juveniles ate crabs more than adult males did.
608 Why crab-fishing was sex-biased is an important question that could help understand
609 sex and age differences in other foraging strategies.
610
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625 **FIGURE LEGENDS**

626

627 **Figure 1.** Map of study site with crab-fishing sites (N = 4, crab symbols) and control
628 sites (N = 8, red circles).

629

630 **Figure 2.** Still images from motion-triggered camera video of an adolescent male
631 chimpanzee crab-fishing (Suppl. Video 2): searching (a), and eating (b) crab.

632

633 **Figure 3.** Remains of large crabs discovered on 4th of August 2012 (a) *Liberonautes*
634 *latidactylus*, and on 18th of May 2013 (b) *L. rubigimanus*.

635

636 **Figure 4.** Chimpanzee crab-fishing site visiting rates (red line) and rainfall (a), fruit
637 availability (b), and ant-dipping (c). Numbers above ant-dipping bars indicate the
638 number of fecal samples collected per month.

639

640 **Figure 5.** Proportion of parties belonging to different party types for crab-fishing
641 parties (CF, grey) and non-crab-fishing parties at control sites (Non-CF, white).

642

643 **Figure 6.** Proportion of crab-fishing parties (female(s) and offspring *vs.* other parties)
644 fishing for <1 min, 1 – 10 min, 10 min – 1 hr, and >1 hr.

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